

SPATIAL AND TEMPORAL GENETIC STRUCTURE OF WILD EMMER WHEAT IN JORDAN. I. PHENOTYPIC TRAITS

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ABSTRACT

Natural populations of wild emmer wheat in Jordan represent a unique and sizable part of the species' distribution in the Fertile Crescent. However, information on their genetic structure and diversity is limited. An understanding of the way genetic variation is partitioned among these populations is of primary importance for the ex situ sampling and in situ conservation of their genetic diversity. Fourteen categorical traits were used to characterize different phenotypes found in 12 wild emmer wheat populations in Jordan. They were scored in plants growing in 207 marked sampling sites and representing a wide range of observable variation. A strong effect of the heterogeneous habitats, encountered across collecting sites, was reflected in the magnitude and spatial distribution of phenotypic diversity. Several, and probably unique, first- and second-order associations among phenotypic traits reflect functional adaptation of the species to arid and semiarid Mediterranean environments. Phenotypic distances among populations were highly influenced by latitude and rainfall quotient (Q2) of collection sites. Spatial factors accounted for large portions (60.5–93.1%) of total variation in phenotypic diversity indices, suggesting strong provenance specificity. Temporal variation was less pronounced than spatial variation, and there were no drastic changes between years in frequencies of genotypes. Both spatial and temporal variation varied among populations.

INTRODUCTION

It is now well established that Neolithic agriculture, developed in the Middle East, depended primarily on the domestication and subsequent cultivation of wild einkorn and emmer wheat, and wild two-rowed barley (Sakamoto, 1982, Zohary and Hopf, 1993). Natural populations of wild emmer wheat, *Triticum turgidum* L. ssp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell., are confined to the Fertile Crescent (Zohary and Hopf, 1993). The species has its center of origin and center of diversity, and attains its widest morphological variation and ecological range in Israel (Nevo et al., 1984), Jordan (Jaradat, 1987), and southern Syria and Lebanon (Valkoune et al., 1992).

Wild emmer wheat is more demanding in its require-

ments than wild einkorn or wild barley, is not a weedy plant, is never a dominant species, and its present-day distribution is discontinuous (Zohary and Hopf, 1993). This very discontinuity suggests that the species now occurs less widely than in earlier times. Harlan (1992) suggested that it may have been displaced during the ice age downslope in the Zagros Mountains towards the south. The fact that wild emmer wheat has been found at Cayonu, Turkey, also suggests a rather wider distribution some 10,000 years ago.

Natural populations of wild emmer wheat in the catchment area of the Upper Jordan Valley are common,[†]Present address: Plant Genetic Resources Program, International Center for Biosaline Agriculture, ICBA P.O. Box 14660, Dubai, UAE.
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lush, and continuous in their spread. However, elsewhere in the Fertile Crescent, populations of wild emmer wheat are semi-isolated and isolated, and largely display a patchy structure; in this region, wild emmer wheat populations are subdivided into demes or clumps of varying sizes (Nevo and Beiles, 1989). Wild emmer wheat populations have been collected over a wide altitudinal amplitude (180 m below to 1600 m asl), and they grow on soil types of basaltic hard limestone, and dolomitic bedrock. Nevo et al. (1982, 1984) concluded that the species is restricted to primary habitats and grows together with wild barley and wild oats.

The extraordinary biotic and abiotic diversity in the Fertile Crescent has resulted in a wide range of adaptive diversity to these stresses, both within and among populations of wild emmer wheat throughout its distribution (Anikster et al., 1991; Valkoun et al., 1992; Jaradat, 1997).

The geographical distribution of wild emmer wheat in Jordan (Table 1) encompasses central, peripheral, and marginal populations of the species not represented elsewhere in the Fertile Crescent (National Atlas of Jordan, 1984; Jaradat, 1997). Central populations thrive in favorable but heterogeneous environments and were found to be more diverse than marginal or peripheral ones, especially in readily observable traits, such as glume color and awn color. Peripheral populations were usually scattered over a large area, while the marginal ones were confined to small patches or were sparsely scattered. In a previous study (Jaradat, 1997), several ecotypes were identified on the basis of quantitative morphological, developmental, and reproductive traits, that were scored in progenies of plants sampled in the field. These ecotypes exhibited different adaptive trait complexes. It was postulated that particular environmental conditions across the distributional range of the species in Jordan, and elsewhere in the Fertile Crescent, have resulted in the evolution of adaptive gene complexes that are conserved by genetic linkage or natural selection. Phenotypic attributes of different true-breeding lines of wild emmer wheat were considered essential in the selection of desirable germplasm for in situ conservation (Anikster et al., 1991). These researchers also emphasized the need for studying the ecological affinities of given phenotypes in order to establish a quantitative relationship between heterogeneous habitats and phenotypic diversity in the species. The present study was designed to complement the existing body of knowledge on the species and reports on the spatial and temporal genetic structure of wild emmer wheat in Jordan, based on 14 qualitative morphological traits. This complementary information should aid the understanding of genetic differentiation and evolution across large

parts of the Fertile Crescent region, and enhance potential application of the wild genetic resources in wheat improvement.

MATERIALS AND METHODS

The same 12 main populations described in a previous study (Jaradat, 1997) were used for the present analyses. A summary of the geographical and ecological characteristics of 12 main wild emmer wheat populations in Jordan is presented in Table 1. Elevation asl of these populations ranged from 550 to 1100 m. No wild emmer wheat populations were found below sea level east of the Jordan River. Average annual rainfall at the collection sites during the study period ranged from 250 mm at Jraineh, near Madaba in central Jordan, to more than 600 mm at two semi-humid populations in the Ajlun (Ishtafina) and Salt (Zaatari) Mountains.

A rainfall quotient, Q_2 (Emberger, 1955), was calculated for each location and is presented in Table 1. It reflects the joint effect of rainfall and temperature on the collection sites. Six sites (Ibbien, Jarash, Jraineh, Naour, Samad, and Umamad) had the lowest Q_2 -values (ranging from 36 to 55), indicating a low rainfall and high temperature regime. Intermediate Q_2 -values (60–65) were found for three populations (Afana, Natfeh, and Sakhra), all in the Ajlun Mountains of northern Jordan. High Q_2 -values (70–75) were characteristic of two populations (Ishtafina and Zobia) in the Ajlun Mountains, and one (Zaatari) in the central Salt Mountains.

Central populations were large in size and highly variable in readily observable characteristics (e.g., glume and awn color). Peripheral populations were usually scattered over a large area and less dense and less variable than the central populations, while marginal populations were confined to small patches or sparsely scattered.

Geographical descriptors (longitude, latitude, altitude) and location characteristics (long-term rainfall average, rainfall quotient, habitats, rock cover, soil texture, aspect, and slope of the collection site) are listed in Table 1. These populations extended from Natfeh in the northwest to Jraineh in the south. The population near Jarash was the easternmost one. Five major habitats were identified across locations: (1) agricultural crop, where wild emmer wheat was found growing in an agricultural field, (2) disturbed habitat, (3) marginal wooded area or forest, (4) roadside, and (5) protected habitat, mostly in an orchard protected by a fence or a stone wall. Rock cover ranged from none in cultivated fields and orchards to >40%, especially in hilly locations. Three broad soil types were identified within locations of the 12 populations. These were: clay, clay–

Table 1
Geographical descriptors for 12 natural emmer wheat populations in Jordan. Based on Table 1 in Jaradat, 1997, with additional data

Eco-region	Location	Long.	Lat.	Alt. m	Rain mm	Q2	Habitat ¹	Rock cover	Texture	Aspect	Slope	
		Decimal										
Central	Ishtafina	35.80	32.35	1,100	600	75	MF	RR (10–20%)	Clay–Loam	Southeast	Undulating	
	Zobia	35.84	32.43	900	450	70	MF	RRR (>40%)	Clay	West	Steep	
Peripheral	Zaatari	35.80	32.07	1,000	600	75	DI	RR (10–20%)	Clay	Southeast	Moderate	
	Afana	35.92	32.38	1,000	500	63	RS	R (<10%)	Silt–Loam	Undulating	Rolling	
	Natfeh	35.70	32.50	750	500	65	MF	RRR (>40%)	Silt–Loam	South	Moderate	
	Sakhra	35.87	32.39	1,000	450	60	AC	R (<10%)	Clay–Loam	Undulating	Undulating	
Marginal	Ibbien	35.88	32.37	900	420	55	MF	RR (10–20%)	Clay–Loam	South	None	
	Jarash	36.00	32.28	600	300	40	DI	R (no rock)	Clay	Southeast	None	
	Jraineh	35.72	31.75	700	250	40	PE	RR (10–20%)	Clay–Loam	West	Steep	
	Naor	35.75	31.80	550	250	36	AC	R (<10%)	Clay–Loam	West	Steep	
	Samad	35.82	32.47	700	350	47	MF	R (no rock)	Clay	South	Rolling	
	Umamad	35.87	32.10	800	300	45	DI	R (<10%)	Clay–Loam	West	Undulating	

¹MF = Marginal forest; DI = Disturbed; RS = Road side; AC = Agricultural crop; PE = Protected

Table 2
Categorical traits scored on wild emmer wheat plants and their description

Categorical trait (abbreviation)	Number and description of categories
Awn length (ANL)	Long (1), Medium (5), Short (9)
Awn color (ACL)	White (1), Brown (5), Black (9)
Fertility of basal floret (FBF)	Fertile (1), Sterile (2)
Flag leaf attitude (FLA)	Erect (1), Medium (5), Horizontal (9)
Leaf attitude (LAT)	Erect (1), Medium (5), Horizontal (9)
Glume color (GCO)	White (1), Brown (5), Black (9)
Glume hairiness (GHR)	Glabrous (1), Low/Medium (5), High (9)
Glume peak shape (GPS)	Shoulder: Absent (1), Oblique (3), Equal (5), Elevated (7), Rounded (9)
Spike density (SDN)	Dense (1), Medium (5), Lax (9)
Spikelets per spike (SPS)	High (1), Medium (5), Low (9)
Growth class (GCL)	Winter (1), Facultative (5), Spring (9)
Juvenile growth habit (JGH)	Erect (1), Medium (5), Prostrate (9)
Plant vigor (PVG)	Healthy (1), Medium (5), Weak (9)
Glaucousness (GLC)	Strong (1), Medium (5), Weak (9)

loam, and silt-loam. Two of the locations were undulating, six faced south or southeast, and the remaining four faced west to northwest. The slope of three locations was steep, that of two locations moderate, five locations were rolling, with gentle ups and downs, or undulating (wave-like), and two locations were level.

GERMPLASM COLLECTION

The plants used for analyses were examined in the field in the course of three years (1988–1990) on the sampling sites of a germplasm collection that represents the main 12 wild emmer wheat populations. In spring 1987, a variable number (9–27) of permanent sampling points had been marked in each of the populations. A total of 207 sampling points had been selected in such a way as to represent variability in observable morphological and developmental characters. In the period 1987–1991, the number of wheat plants growing in a 1 m² plot around each sampling point was recorded during May and June and, at maturity, single spikes from individual plants growing within a 1 m radius of the marked sampling point were collected from all 12 populations. As far as possible, the collections were made from a minimum of 15 plants in each location every year. Smaller samples (~10 plants) were collected during 1988 and 1989 in the marginal populations of Jraqineh and Naour, while the maximum number of plants was 37 in each of the three central populations. In the Ishtafina, Zobia, and Zaatari populations, seed was also collected from the soil seed bank at the end of the growing season in the years 1988–1990. The collection is stored as bulk at the Genetic Resources Unit of the International Center for Agricultural Research in Dry Areas (ICARDIA), Aleppo,

Syria and, as single spikes, at Jordan University of Science and Technology, Irbid, Jordan.

COLLECTION OF FIELD DATA

Qualitative traits recorded for each plant sampled during the study period are listed in Table 2, together with the number and description of classes used for categorical classification. These traits can be divided into four broad groups: (1) awn length and color, and glume color, glume peak shape, and hairiness; (2) flag leaf and penultimate leaf attitude, and glaucousness (waxiness); (3) spike density, spikelets per spike, and fertility of basal spikelet; and (4) plant vigor, juvenile growth habit, and growth class.

STATISTICAL ANALYSIS

The polymorphic index, as described by Zhang and Allard (1986), was calculated from relative frequencies for each of the 14 categorical traits and 12 populations during the three-year sampling period. The adjustment in phenotypic diversity indices suggested by Zar (1996) was implemented to account for differences in the number of phenotypes (two in fertility of basal floret to five in glume peak shape), and testing for differences between two diversity indices was carried out according to Hutchinson (1970). Tests of independence of pairs of categorical traits, populations and traits, and years and traits were performed using standard two-way contingency chi-square tests. Associations among more than two categorical traits were tested using log-linear models (Agresti, 1990), as implemented by StatSoft (1998). However, the number of traits used for the log-linear models was limited to four in order to reduce the complexities of data analysis and interpretation. Due to the

Table 3

Analysis of variance and variance components in phenotypic diversity indices of 14 categorical traits scored on wild emmer wheat plants in 12 natural populations in Jordan, accounted for by populations

Trait ¹	Phenotypic diversity index		Values of <i>p</i> among populations	% Sig. diff. among populations N = 66	% Variance due to populations	z	Asymptotic <i>p</i>
	Mean	SE					
ANL	0.479	0.0196	0.895	0.0	33.0	1.58	0.113
ACL	0.472	0.0372	0.137	0.0	10.0	1.02	0.213
FBF	0.325	0.0189	0.156	1.81	49.0	2.02	0.045
FLA	0.443	0.0301	0.000	5.45	63.3	2.28	0.022
LAT	0.448	0.0305	0.003	9.00	71.7	2.41	0.015
GCO	0.814	0.0199	0.000	27.3	72.9	2.43	0.015
GHR	0.345	0.0214	0.008	5.45	74.3	2.44	0.014
GPS	1.019	0.0327	0.000	21.8	52.9	2.08	0.037
SDN	0.533	0.0262	0.005	10.9	58.8	2.20	0.027
SPS	1.275	0.0213	0.004	12.7	41.8	1.83	0.062
GCL	0.632	0.0345	0.000	3.60	54.7	2.30	0.021
JGH	0.733	0.0253	0.001	27.3	60.2	2.22	0.025
PVG	0.941	0.0269	0.000	18.10	66.2	2.32	0.019
GLC	0.739	0.0421	0.000	12.7	58.2	2.35	0.018

¹See Table 2 for abbreviations.

complexity arising from the large number of the four-character associations, a preliminary selection of interaction terms was performed, and a basic log-linear model consisting of only significant interaction terms was constructed. These log-linear models were tested, using the likelihood ratio (G^2) tests, as described by Agresti (1990) and Sokal and Rohlf (1995). A polymorphic distance, analogous to genetic distances based on

allozymes and HMW-glutenins, was calculated for the 12 populations, using frequencies of all 14 categorical traits. The computer program "POPGENE, V. 1.31" (Yeh et al., 1999) was used for calculating diversity indices for the 14 phenotypic traits, and a "standard phenotypic distance", analogous to genetic distances based on allozymes and HMW-glutenin loci, was calculated for each population.

Table 4

Significant variance components (% of total variance) in 14 categorical traits scored on wild emmer wheat plants and accounted for by year, habitat, rockiness, soil texture, aspect, and slope of 12 collection sites in Jordan

Trait ¹	Variance components (<i>p</i> < 0.05) due to:						Cumulative variance %
	Year	Habitat	Rock cover	Soil texture	Aspect	Slope	
ANL	11.2	38.2	–	9.8	11.6	13.8	84.6
ANC	–	39.1	12.6	–	–	11.2	62.9
FBF	–	47.9	–	–	9.0	17.5	74.4
FLA	–	22.8	12.4	10.9	11.0	25.6	82.7
LAT	–	22.2	–	15.9	15.2	31.6	84.9
GCO	–	45.4	15.1	–	–	–	60.5
GHR	–	21.2	22.9	–	12.7	32.1	88.9
GPS	–	60.6	–	9.5	10.0	13.0	93.1
SDN	–	41.6	–	–	10.2	19.8	71.6
SPS	10.3	54.1	–	–	9.3	9.8	83.5
GCL	–	19.2	–	–	13.6	35.2	68.0
JGH	–	38.1	–	14.8	–	32.5	85.4
PVG	–	57.1	–	11.5	10.5	11.7	90.8
GLC	–	19.2	13.9	–	12.8	30.7	76.6

¹See Table 2 for abbreviations.

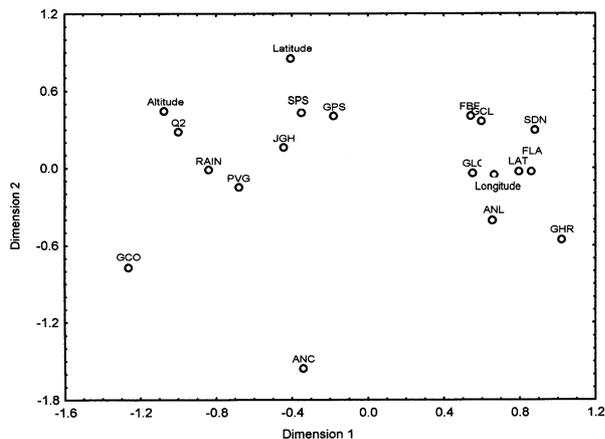


Fig. 1. A two-dimensional plot of 14 categorical traits, scored on wild emmer wheat plants in 12 natural populations from Jordan, together with coordinates, average long-term rainfall, and rainfall quotient of collection sites. For abbreviations, see Table 2.

RESULTS

PHENOTYPIC VARIATION

Summary results of the analysis of variance and estimation of variance components of the phenotypic diversity indices for 14 categorical traits are presented in Table 3. The mean phenotypic diversity index and its standard error arbitrarily separated these traits into three groups: the first with phenotypic diversity indices higher than one (two traits), the second group with intermediate (0.6–0.9) phenotypic diversity indices (six traits), and the third with low (<0.6) phenotypic diversity indices (six traits). The most diverse trait was spikelets per spike (SPS), while the least diverse was fertility

of the basal floret (FBF). Differences among populations in the phenotypic diversity index were significant for 12 of the 14 categorical traits (Table 3). However, the magnitude of these significant differences among populations, as expressed by the percent of significant differences for all 66 possible pairwise comparisons among 12 populations [i.e., $n(n-1)/2$], varied from very small (1.81%) for FBF to intermediate (27.3%) for each of glume color (GCO) and juvenile growth habit (JGH).

The variance component due to populations, i.e., the ‘population covariation’ between the wild emmer wheat populations and the phenotypic diversity index for each of the 14 categorical traits, ranged from 10.0% for awn color (ACL) to >70% for each of leaf attitude (LAT), glume color (GCO), and glume hairiness (GHR). Significance tests for the variance component, as seen from the values of z and an asymptotic value of p in Table 3, indicate that a sizable portion of the variability in phenotypic diversity indices was accounted for by differences among populations; only two z -values were non-significant (awn length, ANL, and awn color, ACL), while a third (spikelets per spike, SPS) was significant at $p = 0.062$.

Differences in the 14 phenotypic diversity indices due to characteristics of collection sites were estimated and subjected to variance component analysis (Table 4). Five spatial factors (location characteristics: habitat, rock cover, soil texture, aspect, and slope) and one temporal factor (year) accounted for a significant ($p < 0.05$) minimum of 62.9% to a maximum of 93.1% of total variation in the phenotypic diversity index estimates. In most traits, habitat was the most important single factor in accounting for maximum variation (range 19.2–60.6%). It was followed by the slope of collection site, which accounted for a minimum of 9.8 to

Table 5

Simplest log-linear models based on two-way and three-way associations of 14 categorical traits scored on wild emmer wheat plants in 12 natural populations in Jordan

Models	Conditionally dependent traits ¹
Two-trait associations	[ANL-SPS], [FBF-SPS], [SPS-ANC], [SPS-GPS], [SPS-GHR], [SPS-GCO], [SPS-SDN], [FLA-PVG], [LAT-PVG], [GLC-PVG], [GLC-FBF], [JGH-FBF], [GCL-FBF], [GCO-PVG], [GHR-GLC], [GHR-FLA], [GHR-GCL], [GHR-JGH], [GHR-PVG], [GHR-GLC], [GCL-GLC], [SPS-PVG], [SPS-GLC], [GLC-FLA].
Three-trait associations	[ANL-GPS][GPS-FBF][FBF-ANL], [GHR-FBF][FBF-ANC][GHR-ANL], [GPS-FBF-ANL][GCO-GPS-ANL], [SDN-GPS-FBF][SDN-GPS-ANL][ANL-FBF], [GHR-GPS-FBF][GCO-GHR-GPS][GCO-GHR-FBF], [GCL-JGH-PVG][JGH-GLC], [GLC-FBF-GCO][GLC-FLA][SPS-GLC], [GLC-GCO-GPS][GLC-FBF-GPS][GLC-GHR-FBF]

¹See Table 2 for abbreviations.

a maximum of 35.2% of the variation in diversity index estimates. The temporal factor (year) accounted for a small portion of the variation in only two of the estimates (awn length and spikelets per spike).

The phenotypic diversity index for glume color was the only one to be significantly influenced by only two of the spatial factors, i.e., habitat and rock cover, which accounted for 45.4% and 15.1% of the total variation in this index, respectively. Most phenotypic diversity indices were significantly influenced by three (five traits) or four (seven traits) spatial factors, while the diversity index for flag leaf attitude was the only one to be influenced by all five spatial factors.

The correlation matrix between diversity indices of phenotypic traits and each of the parameters longitude, latitude, Q2, and average rainfall of the collection site were utilized in a multidimensional scaling analysis. Results are presented in Fig. 1. More than half (56.7%) of the 120 pairwise correlation coefficients among the 16 variables were highly significant. Diversity indices of eight of the 14 categorical traits were highly and significantly correlated with longitude, four with latitude, three with average rainfall, and six with Q2. In the final configuration, most phenotypic traits were clustered around longitude and latitude of the collection site. A lesser number occurred close to Q2 and average rainfall of the collection site. The first dimension separated eight traits highly associated ($p < 0.01$) with longitude (FBF, $r = 0.588$; GHR, $r = 0.450$; SDN, $r = 0.471$; FLA, $r = 0.545$; LAT, $r = 0.567$; GCL, $r = 0.396$; GLC, $r = 0.577$, and ANL, $r = 0.409$) from those highly associated with latitude (GPS, $r = 0.563$; SPS, $r = 0.516$; JGH, $r = 0.396$; and PVG, $r = 0.482$); whereas dimension 2 totally separated the traits awn length (ANL), awn and glume color (ACL, GCO), and glume hairiness (GHR) from the rest; the remaining traits were only marginally separated. Two traits, GHR and PVG, were significantly ($r = -0.533$ and 0.302 , respectively) correlated with the altitude of the collection site.

PAIRWISE ASSOCIATIONS AMONG CATEGORICAL TRAITS

Tests of the independence of pairs of categorical data were performed, using the standard two-way contingency chi-square statistic. A small number (seven) of the total 91 two-way contingency chi-square tests involving the 14 categorical traits, appeared independent. Four of the independent associations involved the trait spikelets per spike in association with each of growth class, juvenile growth habit, plant vigor, and glaucousness. The remaining three independent associations involved plant vigor and its association with each of awn color, awn length and glume peak shape. It can be

concluded that bivariate associations in wild emmer wheat are generally the rule rather than the exception.

The log-linear analysis (Agresti, 1990), a discrete multivariate analysis technique most appropriate for elucidating the organization of multi-trait associations, was adopted for the analysis of three and four categorical traits. In order to reduce the complexities of categorical data analysis and interpretation, the number of traits used in the log-linear analysis was limited to four. A preliminary selection of interaction terms was constructed and a basic log-linear model consisting of only significant interaction terms was constructed. The likelihood ratio statistics (G^2) were then calculated for the respective log-linear models and tested for the goodness-of-fit of these models. The final models included traits listed in Table 5. The 'best-fitting' models included 24 two-trait association terms, 8 three-trait association terms and no four-trait association terms. However, three different traits appeared in only two of the eight three-trait log-linear models, four different traits in three different models and five different traits in the remaining two models (lower part of Table 5).

As can be seen in Table 5, the traits: spikelets per spike, glaucousness, and glume hairiness appeared in at least seven of the final 2-trait models; whereas fertility of basal floret appeared in seven, glume peak shape in five and glume color in four of the final eight three-trait log-linear models. Other traits, e.g., spike density and awn length, were involved in multi-trait associations to a greater extent than the remaining traits considered in the log-linear analysis.

SPATIAL DISTRIBUTION PATTERNS OF PHENOTYPIC TRAITS

A chi-square test was employed in testing for spatial distribution patterns of categorical traits in wild emmer wheat (Table 6). p values indicate that certain phenotypes (categories, character states) of these traits displayed higher frequencies than those expected under the null hypothesis, and proved to be highly associated with certain locations (provenance specificity), while other phenotypes were independently distributed across locations. For example, genotypes with fertile basal florets were more confined to central, more mesic (Ishtafina, Zobia, and Zaatari) than to xeric locations (e.g., Jraineh and Naor). Populations differed as to the number and predominance of phenotypes of categorical traits. Mesic populations (Ishtafina, Zobia, and Zaatari) displayed larger numbers of phenotypes of a given trait and, to some extent, similar phenotypes of that trait, than the more xeric populations (e.g., Jraineh and Naor). Moreover, in some populations, certain phenotypes of two or more categorical traits appeared to be more closely associ-

Table 6
 Spatial distribution patterns of qualitative traits scored on wild emmer wheat plants in 12 natural populations in Jordan. Numbers refer to categories with significantly greater than expected frequencies

Trait ¹	Ishtafina	Zobia	Zaatari	Afana	Natfeh	Sakhra	Ibbien	Jarash	Jraineh	Naor	Samad	Umamad	χ^2	df	<i>p</i>
ANL	5					1		1			1		22.4	10	.010
ANC			1		9	5							63.8	30	.000
FBF	1	1	1		1		2	2	2	2	2		51.3	10	.000
FLA		9	9	1	1	9	1	1					80.11	24	.000
LAT			5,9	1		9	1	1					85.6	15	.000
GCO	5	1	1			5	5		1			1	315.3	20	.000
GHR	1	1	1		5								156.3	20	.000
GPS	7	5	1		3	5	7			1		1	298.5	40	.006
SDN	1	9	9		5	9	9	9					95.5	20	.000
SPS	1	1	1		5			9	9	9		5	102.3	40	.000
GCL	9	1,9	1,9	9		9	5				9		194.7	30	.000
JGH	5	1	9		5	9		1	9		5	9	163.2	30	.000
PVG	9	5	1	9	5	9	5			1	5	1	76.3	30	.000
GLC	9	9	5	1	1	9	5	5	9	9	5	9	191.5	30	.000

¹See Table 2 for abbreviations.

Table 7
Temporal distribution patterns of qualitative traits scored on wild emmer wheat plants in 12 natural populations in Jordan

Trait ¹	Year 1	Year 2	Year 3	χ^2	df	<i>p</i>
	1	2	3			
ANL	–	5	1	5.82	4	0.120
ANC	1	5	1	85.5	4	0.000
FBF	–	–	–	.079	2	0.990
FLA	5	9	–	.173	4	0.916
LAT	5	–	–	.096	4	0.952
GCO	5	1	5	4.33	4	0.631
GHR	–	1	–	26.8	4	0.090
GPS	–	1	7	21.9	10	0.078
SDN	9	5	–	13.4	4	0.086
SPS	1	5	1	26.2	4	0.010
GCL	1	–	5	3.40	4	0.490
JGH	9	–	5	3.52	4	0.478
PVG	1	5	9	4.42	4	0.350
GLC	5, 9	1, 5	9	2.81	4	0.590

¹See Table 2 for abbreviations. ²Numbers refer to categories with significantly greater than expected frequencies.

ated with each other and more predominant than in others. Glumes with brown color were associated with the elevated glume peak phenotype in two populations (Ishtafina and Ibbien), while glumes with an absent shoulder appeared to be associated with the white (straw) glume color in Zaatari. Glabrous glumes were characteristic of genotypes with fertile basal florets in mesic populations, while strong glaucousness was characteristic of genotypes with erect flag leaves in the more xeric populations of Afana, Natfeh, Ibbien, and Jarash. On the other hand, certain phenotypes (e.g., brown glume color, lax spikes) appeared in both mesic and xeric populations. Spring growth types were predominant in most populations; however, both spring and winter growth types appeared to be abundant in two populations (Zobia and Zaatari), where they were sampled at full maturity in June (spring type) and August (winter type), respectively.

It can be inferred from data in Table 6 that the majority (39) of the original 43 phenotypes (character states; see Table 2) were location-dependent and appeared with frequencies higher than would be expected under the null hypothesis. Also, central populations, as a group, displayed more phenotypes than peripheral or marginal populations (e.g., 15 phenotypes in Zaatari and five phenotypes in each of Naor and Jraineh).

TEMPORAL VARIATION IN PHENOTYPIC TRAITS

Temporal variation was much less pronounced than spatial variation in all 14 categorical traits. Over a three-

year period, only two traits (awn color and spikelets per spike) showed a significant change in the frequency of certain phenotypes (Table 7). Phenotypes with white (straw) awn color appeared more frequently during the first and third years, while those with brown awns exceeded their expected frequency during the second year. Similarly, phenotypes with high and medium numbers of spikelets per spike alternated among years. On the other hand, frequencies of all three glaucousness phenotypes appeared to shift over years. Observed frequencies of the remaining phenotypes listed in Table 7, although exceeding the expected ones (e.g., glume hairiness; $p < 0.09$; glume peak shape; $p < 0.078$; and spike density; $p < 0.086$), were not significant.

DISCUSSION

The multidisciplinary study carried out on 12 populations of wild emmer wheat in Jordan had one major objective to address, namely: to draw a detailed spatial-temporal map of phenotypic and genetic diversity of the species and to quantify the genetic structure and differentiation of the species in a major part of its distribution.

In this context, results of this study will be discussed in relation to the geographic range, regional distribution, breeding system, and seed dispersal mechanisms of wild emmer wheat. Furthermore, the buffering capacity of the 'seed bank', i.e., seed accumulated in the soil over the years, and its role in reducing the fitness uncertainty generated by the 'typical' cyclical or random Mediterranean environments, will be addressed.

PHENOTYPIC DIVERSITY

Plant characteristics conducive to development and survival under the Mediterranean environment of the Fertile Crescent are likely to be common in wild and cultivated plants endemic to this region. The question of obvious interest to students of wheat is: which plant traits, either singly or jointly, reflect the adaptation of wild emmer wheat to arid and semi-arid Mediterranean environments? The answer to this question was sought in this study, albeit indirectly, by comparing the frequency distribution and phenotypic diversity indices of 14 categorical traits scored in wild emmer wheat plants in 12 locations in Jordan, their spatial and temporal patterns, and the single and combined effects of a number of ecological variables on them.

Most, if not all, of the 14 categorical traits may merit testing because they are potentially useful in a wheat breeding program. Phenotypic diversity per se is highly desirable in an in-situ reserve of wild species (Anikster et al., 1991) or in on-farm conservation of cultivated species. Moreover, some of these traits have direct relevance to wheat breeding. Phenotypic traits controlled by a single gene can be used as markers of linked quantitative trait loci with desirable alleles (Levy and Feldman, 1989).

It is noteworthy that there were highly significant differences among populations for most of the traits under study. The variability in phenotypic diversity indices and the underlying nonrandom spatial distribution of certain phenotypes, i.e., their ecological affinities, point to the strong effects of heterogeneous habitats on the magnitude and spatial distribution of phenotypic diversity. The more variable the site was (e.g., Ishtafina, Zobia and Zaatari, Table 6), the more traits were found with higher frequencies than those expected by chance. The variable and highly significant variance components in phenotypic diversity indices (Table 4), accounted for by differences among five characteristics of wild emmer wheat locations, support this conclusion and confirm that variable traits in this selfing species with restricted gene flow are expected to have a patchy rather than diffuse distribution (Anikster et al., 1991; Foré and Guttman, 1995).

MULTI-TRAIT ASSOCIATIONS, SPATIAL, AND TEMPORAL DIVERSITY

Tests of independence of pairs of categorical traits, using standard two-way contingency chi-square methods, and log-linear models to elucidate the organization of three or more categorical traits, indicated that bivariate trait associations are the rule rather than the exception. Moreover, during its long history in the Mediterranean environment of the Fertile Crescent, wild emmer

wheat has developed several probably unique first- and second-order associations among the phenotypic traits under study. In the context of in situ or ex situ conservation it is vitally important to rule out a fixed chance association among phenotypic traits, otherwise curators will be misled by plant responses to natural and man-made selection (van Tienderen, 1989).

The phenotypic multi-trait combinations (Table 5) could be co-adaptive and held together by natural selection under specific conditions of the collection sites (Anikster et al., 1991); however, the possibility that these traits are invariably associated as a result of pleiotropy or close linkage (Hamrick and Allard, 1975; Levin, 1978) is yet to be addressed.

Founder effects (Hamrick, 1987), suspected to have an impact on gene flow in a few of the 12 populations (see Jaradat, this issue), may have caused habitat specificity which can be deduced from the spatial distribution patterns and conditional dependency data presented in Table 6. Anikster et al. (1991) concluded that topography, at micro- and macroscales, was an important determinant of habitats in the in situ conservation site of wild emmer wheat at Ammiad, Israel.

Functional adaptation can be inferred from the combined data presented in Tables 3, 6, and 7. For example, flag leaf attitude (erect vs. horizontal) with a diversity index of 0.443 and a few among-location differences (5.45%), but with a large portion of this diversity (63.3%) being accounted for by differences among locations, can only point to functional adaptation. Phenotypes with a horizontal flag leaf and with usually broad leaves and a large number of spikelets per spike (see below) were characteristic of the resource-unlimited and mesic locations of Zobia and Zaatari, while erect, narrow flag leaves were more largely confined to the resource-poor and xeric locations of Ibbien and Jarash. The same conclusion can be derived from data on glume hairiness, spikelets per spike, and glaucousness.

Temporal variation was evident in two of the 14 phenotypic traits under study. Awn color and spikelets per spike (a transformed quantitative reproductive trait, highly influenced by the environment) displayed considerable variation among years. Awn color varied mainly in three locations (Zaatari, Afana and Sakhra) and spikelets per spike in eight of the 12 locations. The remaining traits showed little temporal variation and can be considered as having a range of provenance specificities (Anikster et al., 1991, 1998). Nonetheless, the probability of this temporal variation being a result of sampling alternative phenotypes from the site during the three-year period or, alternatively, an expression of differential fitness (Epperson, 1990; Ellstrand and Elam, 1993) warrants clarification.

It is expected that traits with marked provenance specificity will show little, if any, temporal variation (e.g., growth class, glaucousness); long-term stabilizing natural selection may have reduced, or even eroded, any phenotypic variation for these traits in the soil seed bank. Moreover, the magnitude of temporal fluctuation is expected to be inversely related to the degree of adaptation of a trait to the environment. On the other hand, the large diversity indices found for some of the structural traits (e.g., glume color, glume peak shape; Table 3), together with large population size, may explain the small temporal fluctuations displayed by these and similar traits (e.g., spike color) (Anikster et al., 1991).

The preponderance of the robust ecotype in central populations of wild emmer wheat in Jordan (Jaradat, 1993) and Israel (Anikster et al., 1991; Poyarkova et al., 1991) may have been, directly or indirectly, brought about by ecological conditions of the three central locations in Jordan and, for example, by ecological conditions of the Lower-karst habitat at Ammiad (Anikster et al., 1991). This ecotype exhibited a strong provenance specificity at all three central locations; the large number of spikelets per spike of this ecotype was associated with dense spikes in one population (Ishtafina), while it was associated with lax spikes in the other two (Zaatari and Zobia, Table 6). On the other hand, populations at the marginal locations (Jarash, Naor, Samad, and Umamad) were at the other end of the spectrum, with short spikes and low number of spikelets per spike.

It is expected that the detailed record of phenotypes and their spatial-temporal variation patterns in this and other studies on wild emmer wheat in the Fertile Crescent (Nevo, 1983; Anikster and Noy Meir, 1991; Heyn and Waldman, 1992; Anikster et al., 1998) will form an integral part of the database that can serve future strategies for in situ conservation of the species on a regional scale.

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